TRANSDUCTION OF NANOVOLT SIGNALS: LIMITS OF ELECTRIC-FIELD DETECTION

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Life scientists of diverse backgrounds gathered in La Jolla, California, for three days in November 1989 to discuss the extreme electrical sensitivity of marine sharks, skates, and rays. The meetings were held at the Scripps Institution of Oceanography under the auspices of the Office of Naval Research, Igor Vodyanoy, Scientific Officer, Ad. J. Kalmijn, Convener.

After reviewing the results of earlier studies on the electric sense at the animal and system levels, the participants discussed the basic process of signal transduction in terms of voltage-sensitive ionic channels. Struck by the small charge displacements needed for excitation, they strongly recommended that sensory biologists, physiologists, and biophysicists join in a concerted effort to initiate new research on the ionic mechanisms of electric-field detection. To obtain detailed information on the electroreceptive membrane and its ionic channels, high-resolution recording techniques will be mandatory.

Marine elasmobranch fishes detect dc and low-frequency electric fields as weak as 5 nV/cm. The animals rely on their acute electric sense when homing in on the common bioelectric fields of prey, in orienting to the electric fields of ocean currents, and, perhaps, even in sensing their magnetic compass headings by detecting the fields they themselves induce when moving through the earth's magnetic field (Refs. 3, 4). Other, e.g., electrochemical and electrokinetic, fields may provide significant sensory cues as well.

The oceans' electric fields indeed present a wealth of sensory information. Nevertheless, as a group, apparently only the elasmobranch fishes have developed the sensory apparatus -- consisting of the ampullae of Lorenzini -- necessary to take full advantage of this sensory modality in the marine habitat. Scattered families of freshwater fishes either detect environmental electric fields that are about two orders of magnitude stronger, or they operate at higher frequencies in response to discharges of specialized electric organs.

The high electrical sensitivity of elasmobranch fishes is dictated by the low strengths, in terms of voltage gradients, of the signals in the oceans. The limits of electric-field detection are set by the noise per bandwidth of the sensory system and, ultimately, by the quantal nature of the ionic charge carriers. It is still uncertain, however, whether the transduction process is based on a refinement of familiar ion-channel kinetics, or whether the system functions in a different, more sophisticated manner.

The ampullae of Lorenzini are located in the head region. Each ampulla (Fig. 1) connects to the seawater by a jelly-filled canal, up to several centimeters in length, leading to a small pore in the skin. Important sources of noise are the receptor cells in the ampulla proper and the jelly of the ampullary canal. The thermal noise of the canal is coherent with regard to the receptor cells; the physiological noise of the individual receptor cells, however, is incoherent and may be reduced effectively by peripheral and central averaging. The noise of the many ampullary organs naturally is incoherent as well.

In addition to signal averaging, the animals may follow several strategies of active bandwidth reduction to enhance the relevant electrical signals and to suppress environmental and system noise. Sharks may need the full dc to 8 Hz system bandwidth to detect the steep, transient signals when approaching prey. In orientation, however, the signals resulting from the animals' swaying mode of locomotion through electric and magnetic fields are periodic. Since they are under direct control of the recipient animal, these signals lend themselves excellently to bandwidth reduction by coherent detection.

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Moreover, the animals need not analyze the incoming signals in full detail to suppress noise but may focus on the salient stimulus features expected on the basis of former experience. In predation, for instance, the apparent rotation of the electric field with respect to the body axes during the early stages of the approach may offer less noisy sensory cues for guiding the animals to their targets than the weak intensity gradients of the source fields, although the intensity gradients may become more conspicuous and useful close to the source.

Notwithstanding the several strategies of noise suppression, it remains to be explained how the receptor-cell membrane detects threshold signals of 50 nV or less, calculated for environmental fields of 5 nV/cm known to elicit meaningful behavioral responses in small stingrays having their ampullary pores maximally 10 cm apart. Theoretically, a 50-nV threshold stimulus in the form of a step function yields a threshold current through the 8 um^2 apical membrane of each receptor cell (Fig. 2) of an estimated 12 electron charges per second.

The number of electronic charges needed to excite the receptor cells give direct hints as to the kinds and numbers of ionic channels involved (Ref. 2). At most two ionic channels per cell per second can be opened if each channel requires transmembrane transport of 6 gating charges, or four channels for 3 gating charges, etc. The channels that open must give rise to further depolarization of the apical membrane, perhaps in cooperation with the basal membrane of the receptor cell by positive feedback (Ref. 1). Since the ampullary nerve fibers are spontaneously active, no absolute threshold exists unless the system is limited by the quantal nature of the ionic charges.

The highest electrical sensitivity known in the Animal Kingdom demands full attention in its own right. Most excitable cells apparently operate at voltage levels sufficiently far from the limits of electric-field detection to be relatively insusceptible to the effects of noise and interference; conversely, other excitable cells may respond to lower electric-field levels than has been thought possible. Hence, man-made fields may be relatively harmless to most, but not to all cells, tissues, and organs of the human body.

The electroreceptive membranes also provide a unique opportunity for comparing the ionic mechanism of the animals versus the electronic mechanism of solid-state devices that have been adapted to detecting oceanic electric fields by use of ionic/electronic electrode interfaces. Operating near or, perhaps, at the limits of electric-field detection, marine sharks, skates, and rays set the Navy a real-life example of how to detect underwater objects at short range by sensing and appropriately processing their electric fields.

At the meetings, Charles S. Cox described the oceans' electric fields. Ad. J. Kalmijn, Carl D. Hopkins, and Harold H. Zakon reviewed the electric sense at the animal and system levels. Michael V. L. Bennett and William T. Clusin detailed the physiology of the receptor epithelia and sensory cells. Harvey M. Fishman and James C. Weaver discussed the electrical properties of excitable membranes. Maurice S. Montal and William F. Gilly considered the kinds of ionic channels likely to be involved. Leon J. Brunner and Charles N. Rafferty took an active part in the ensuing discussions. Robert Newburgh and Igor Vodyanoy outlined Navy needs. David W. Adelson served as the workshop secretary.

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Legends

Figure 1. Ampulla of Lorenzini. Ampullary canal (cut), sensory lobules of ampulla proper, and afferent nerve fibers. The walls of the lobules constitute the single-layered sensory epithelia, see Fig. 2. (After Waltman, Ref. 5.)

Figure 2. Sensory epithelium with pear-shaped receptor cells (clear) lodged between supporting cells (shaded). Each receptor cell has a true kinocilium (kc) protruding from the apical membrane into the ampullary jelly. The apical contacts between cells of the sensory epithelium feature tight junctions (tj). Afferent nerves form synapses (sn) at the basal membranes of the receptor cells. Sensory transduction takes place at the small apical membranes. The function of the kinocilium is unknown. (After Waltman, Ref. 5.)

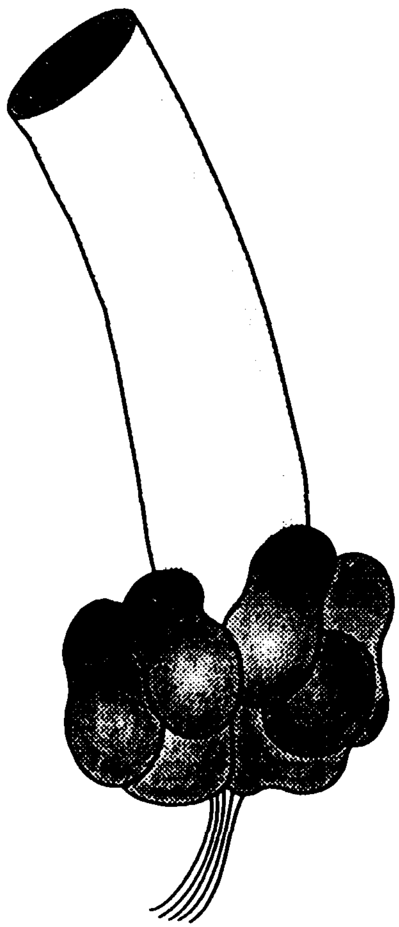
fig. 1

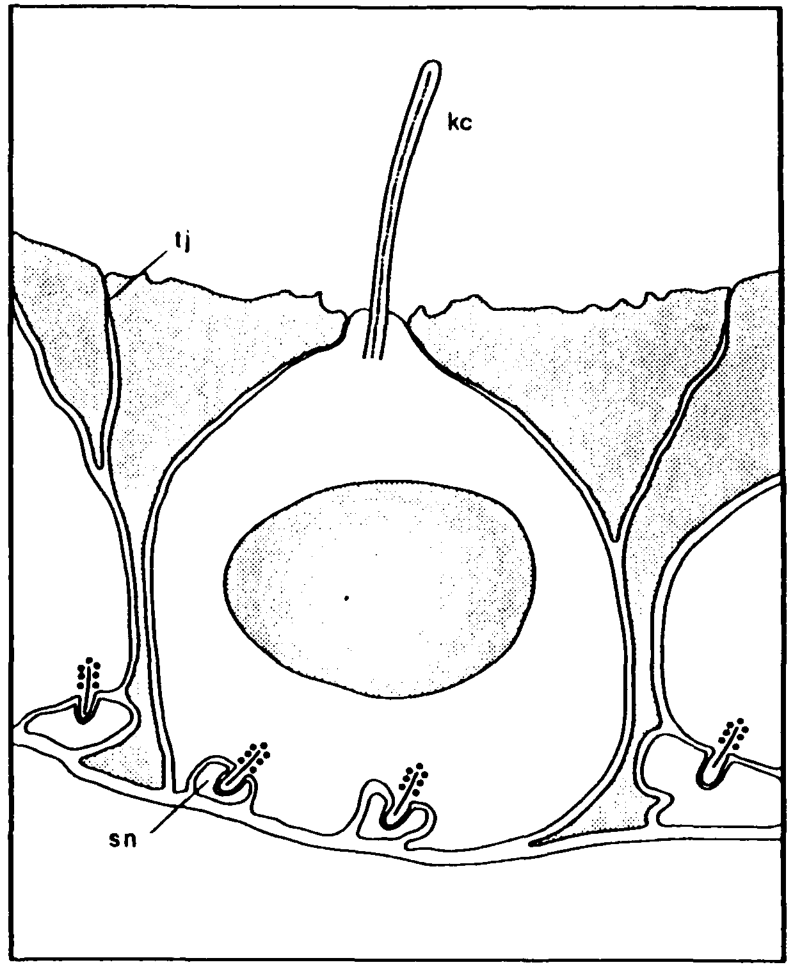

fig. 2